

Characterizing Manatee habitat use and seagrass grazing in Florida and Puerto Rico: implications for conservation and management

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The Indian River Lagoon on the Atlantic coast of Florida, USA, and the east coast of Puerto Rico provide contrasting environments in which the endangered West Indian Manatee *Trichechus manatus* experiences different thermal regimes and seagrass communities. We compare Manatee feeding behaviour in these two regions, examine the ecological effects of Manatee grazing on a seagrass community in the Indian River Lagoon, describe the utility of aerial surveys, radio tracking, and seagrass mapping to study Manatee feeding patterns, and develop hypotheses on sirenian feeding strategies in temperate and tropical seagrass communities. In both the Indian River Lagoon and Puerto Rico, Manatees were typically observed grazing in water depths ≤ 2.0 m and more frequently on the most abundant seagrasses present in the community: *Halodule wrightii* in the Indian River Lagoon and *Thalassia testudinum* in eastern Puerto Rico. Where both *H. wrightii* and *Syringodium filiforme* were consumed in the Indian River Lagoon, Manatees tended to remove more *S. filiforme* than *H. wrightii* rhizome + root biomass. Even though 80 to 95% of the short-shoot biomass and 50 to 67% of the rhizome + root biomass were removed, grazed patches of *H. wrightii* and *S. filiforme* recovered significantly between February and August. *H. wrightii* may be both more resistant and resilient than *S. filiforme* to the impacts of Manatee grazing. Despite the significantly greater abundance of *T. testudinum* in Puerto Rico, Manatees exhibited selective feeding by returning to specific sites with abundant *H. wrightii*. They also appeared to feed selectively on *T. testudinum* shoots associated with clumps of the calcareous alga *Halimeda opuntia*. We hypothesize that Florida Manatees are less specialized seagrass grazers than Manatees in tropical regions like Puerto Rico. Continued research on Manatee grazing ecology in temperate to tropical seagrass communities will enable better protection and management of these vital and unique marine resources.

Key words: Manatee, Seagrass, Grazing, Herbivore, Florida, Puerto Rico, Conservation, *Trichechus manatus*, *Halodule wrightii*, *Syringodium filiforme*, *Thalassia testudinum*, *Halimeda opuntia*.

INTRODUCTION

SEAGRASSES are one of the most productive plant communities found in shallow tropical and temperate seas world-wide (Phillips and McRoy 1980). Marine vertebrate herbivores have become increasingly recognized for their role as grazers in the ecology of reef and seagrass ecosystems (Vicente *et al.* 1980; Tribble 1981; Zieman *et al.* 1984; Preen 1995; Jackson 1997; Valentine *et al.* 1997; Valentine and Heck 1999). It appears that seagrasses have co-evolved with grazers, developing ecological relationships not unlike those described for terrestrial species (McNaughton 1985).

Green Turtles *Chelonia mydas*, Dugongs *Dugong dugon*, and West Indian Manatees *Trichechus manatus* are the largest herbivores utilizing seagrasses as a primary source of nutrition (Thayer *et al.* 1984; Lanyon *et al.* 1989) and are regarded by many conservation organizations and government agencies as either threatened or endangered. Thus, seagrass conservation is closely tied to the protection and survival of these species. Green Turtles and Dugongs are selective grazers of seagrass, while Manatees are opportunistic, generalist herbivores that feed on a wide variety of freshwater, marine and terrestrial plants (Hartman 1979; Bjorndal 1980,

1997; Lefebvre *et al.* 1989; Marsh *et al.* 1999). Seagrasses are important among the vascular plants which Manatees consume; however, other living requirements, such as temperature, salinity, bathymetry, currents, and shelter from wave action also influence their distribution and movements (Lefebvre *et al.* 1989).

On the Atlantic coast of Florida, the semi-enclosed Indian River Lagoon harbours a large segment of the Atlantic coast Manatee population (Provancha and Provancha 1988). In a 10-year study of Manatee movements and migratory patterns on the Atlantic coast, approximately 85% of the radio-tagged Manatees migrated long distances seasonally, both to and from wintering regions (Deutsch *et al.* 1998). Some Manatees migrate to warmer water refuges in the southern end of the lagoon in Martin County, Florida, where Hobe and Jupiter Sounds provide abundant seagrass beds dominated by *Halodule wrightii* and *Syringodium filiforme* (Kenworthy and Fonseca 1996). In this portion of the lagoon, seagrasses are available for Manatees migrating to south Florida in the late fall, and returning north in late winter or spring.

In contrast to the Indian River Lagoon, Manatees in eastern Puerto Rico spend

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PACIFIC CONSERVATION BIOLOGY Vol. 5: 289–98. Surrey Beatty & Sons, Sydney. 2000.

considerably more time in open-water, tropical marine environments dominated by *Thalassia testudinum* (Rathbun *et al.* 1985). *T. testudinum* normally out-competes *H. wrightii* and *S. filiforme* on the soft-bottom carbonate sediments that typify the shallow, oligotrophic waters of most tropical Atlantic environments (Williams 1990). However, physical, chemical, or biological disturbances can alter the normal successional pattern and either *H. wrightii* or *S. filiforme* will temporarily prevail (Fourqurean *et al.* 1995). These two colonizing species have a higher turnover rate, are more shallow-rooted, and their leaf tissues are qualitatively superior for herbivore nutrition (Cebrian and Duarte 1998). Manatees may prefer the faster growing, early successional species over *T. testudinum*, and may have developed specialized feeding strategies to seek out and "cultivate" the preferred species in a manner similar to that described for Dugongs (Preen 1995; de Jongh 1996). Alternatively, the much larger shoot and root-rhizome biomass of *T. testudinum* is a potentially significant source of nutrition.

The specific objectives of this paper are: 1) to compare the feeding behaviour of West Indian Manatees in two contrasting environments dominated by different seagrass species (Indian River Lagoon and Puerto Rico); 2) to examine the ecological effects of Manatee grazing on seagrass community structure (Indian River Lagoon); 3) to describe and compare different approaches for studying Manatee utilization of seagrass feeding habitats (Indian River Lagoon and Puerto Rico); and 4) to develop hypotheses on sirenian feeding strategies in temperate and tropical seagrass communities. The larger goals are to synthesize and interpret the information from two different field studies in order to improve our understanding of Manatee resource use and develop a means to identify, conserve, and protect critical habitats throughout the range of the species.

METHODS

Indian River Lagoon

Study area

Hobe and Jupiter Sounds are shallow, protected coastal lagoons located in the southern Indian River in Martin County, Florida (27°02'30"N, 80°04'00"W) (Kenworthy and Fonseca 1996). Tidal flow originates from Jupiter Inlet and water depths in the lagoons average 2.1 m with a mean tidal range *c.* 50 cm. Salinity ranges from 28 to 38 ppt and water temperature fluctuates between 17°C in winter and 32°C in summer. These two lagoons lie on the primary seasonal travel route of Manatees moving north and south along the Atlantic coast of Florida. In winter, Manatees regularly utilize the warm

water effluent of the Riviera Beach Power Plant (Reynolds and Wilcox 1986), and when weather and water temperatures permit, disperse northward 20 km to feed on seagrasses in Hobe and Jupiter Sounds (Packard 1981).

Surveys of Manatee habitat use

Aerial surveys for Manatees within the study area were conducted during December 1988 and January and February 1989. The surveys were usually conducted in the morning, following Packard (1981). Each survey took approximately 1 h. Manatee locations were plotted on 1:10 000 scale maps overlain with a grid scale. When a feeding Manatee (indicated by the presence of a sediment plume associated with one or more sedentary Manatees) was sighted from the air, its location co-ordinates (using the base map grid system) were radioed to a ground observer. We also made Polaroid photographs of Manatees seen feeding and used landmarks in the photographs to locate exactly where Manatees had been grazing. Since water clarity was very good throughout the study period, and the outlines of the seagrass beds in the study area were visible from the aircraft, we do not believe that observations of Manatees feeding on seagrasses were depth-biased.

Grazing site samples

Manatee feeding sites were visited by boat on the same day as the aerial survey and examined using either snorkel or SCUBA. Depth and seagrass species were recorded. Depths were corrected to mean water level by reference to a local tide station (Kenworthy and Fonseca 1996). Measurements (length and width) of grazing scars were made when a distinctive grazed patch could be identified.

We documented immediate impacts of grazing at eight feeding sites in 1988 and 15 in 1989 using paired biomass cores collected in grazed and ungrazed patches of *H. wrightii* and *S. filiforme*. The small sample size (2) of grazed *T. testudinum* sites precluded statistical analysis. Short-shoot and rhizome + root biomass were obtained by inserting a 15 cm diameter PVC corer approximately 25 cm into the sediment, capping the top, and extracting the entire sediment plug and plant material. Each core was rinsed free of sediment and sorted by species, short-shoots, and rhizomes + roots. Number of short-shoots per core was determined and the plant material was oven-dried at 60°C to a constant weight.

In order to quantify regrowth and determine recovery rate in grazed plots, short-shoots were counted in 14, 1 m² plots established in grazed areas in February 1989 (immediately after grazing). Three corners of each plot were

marked with 2 cm diameter PVC stakes so that we could relocate and re-examine them in spring (May) and summer (August) 1989. We did not establish paired, reference plots for the 1 m² plots because undocumented regrazing could potentially occur in any of the plots, negating the value of a reference. Relative recovery in May and August was gauged in relation to the number of shoots counted per plot in February.

Data analysis

Because the sample size of grazed and ungrazed biomass pairs for each species was relatively small ($n = 44$ for *H. wrightii*, 24 for *S. filiforme*), data from all sites were pooled to test the main treatment effect (grazed *v.* ungrazed), separately for each species and plant component (number of shoots, shoot biomass, and root + rhizome biomass). Data were classified by pair and treatment and analysed using a two-way ANOVA without replication (equivalent to a t-test for paired comparisons; Pp. 354–59 in Sokal and Rohlf 1981). All shoot count data were square root transformed.

Shoot counts and recovery rates in the 1 m² plots were tested using a split-plot ANOVA with sources of variation representing species, plot (within species), season, and species by season interaction. Species and season were fixed effects; plots were considered to be random effects. Relative plot recovery rates of each seagrass species were expressed as the ratio of spring and summer shoot counts over winter counts. All analyses were performed using the General Linear Model procedure of the Statistical Analysis System (SAS Institute, Inc., 1986).

Puerto Rico

Study area

The primary study sites were located within the Roosevelt Roads Naval Station (RRNS) on eastern Puerto Rico and the island of Vieques, located 9.6 km to the south-east. Waters in the study area are fully marine with temperatures typically ranging from 27 to 30°C, salinity 35 to 36 ppt, and a 0.3 m tidal range. Colour aerial photographs (1:9 600 scale) obtained from the US Navy of coastal waters around RRNS and Vieques Island were used to develop computer-based maps depicting coral reefs and seagrass beds available to Manatees and other marine organisms.

Surveys of Manatee habitat use

Two methods were used to delineate habitat use by Manatees: 1) radio and satellite telemetry, and 2) observations in the field. From April 1992 to May 1996, seven free-ranging Manatees

were captured and fitted with floating transmitters. Each transmitter included a UHF satellite-monitored Platform Transmitter Terminal (PTT), a conventional VHF transmitter, and an ultrasonic beacon. The PTTs, monitored by the Argos satellite-based location and data collection system, were capable of supplying up to six locations per day. Tagged Manatees were periodically located and observed in the field using portable VHF receivers and directional antennas. The precise position of the Manatee was recorded along with water depth, number of accompanying individuals, and direct observations of feeding and food resources utilized.

RESULTS

Indian River Lagoon

Aerial surveys

A total of 111 Manatees were sighted during 11 surveys of Hobe Sound in 1988, and 103 animals during 27 surveys in 1989. A total of 97 Manatees were sighted during six surveys of Jupiter Sound in 1988, and 64 animals during 27 surveys in 1989. In both winters, Manatee sightings were most numerous in the northern and southern sections of Hobe Sound. A total of 72 Manatees observed during the 1989 surveys appeared to be feeding (43% of total sightings). Feeding Manatees were most frequently sighted in protected coves or near land points in Hobe Sound. The majority of Manatees sighted in Jupiter Sound were between the channel and the western (mainland) shore, although feeding was noted along both shores. Feeding sites were generally within 70 m of shore.

Grazing sites

It took 10–40 min. for ground observers to reach feeding locations after they were notified by the aerial observer, and frequently the Manatee(s) observed feeding from the airplane had stopped feeding and moved off the grassbeds by the time the boat observer arrived. The Polaroid photos allowed accurate location by boat of almost all of the sites where Manatees were observed feeding from the plane. The average depth of 29 grazed sites was 0.9 m (range = 0.4–1.6 m). The dimensions of 11 grazed patches investigated in detail tended to be elliptical in shape (4 m × 6 m) with an average area of 27 m². Not all portions of the grazed sites were equally impacted; some areas of the grassbed were cropped, some were gouged and rhizomes were removed from the sediment, and some parts showed no sign of shoot or rhizome excavation. Of the 29 grazed sites assessed in 1989; 19 were exclusively or predominantly *H. wrightii*, eight were *S. filiforme*, and two were *T. testudinum*.

Shoot and biomass removal

Biomass samples were taken at 15 feeding sites in 1989; seven in Hobe Sound and eight in Jupiter Sound. In relation to ungrazed areas, number of short-shoots (square-root scale) and short-shoot and rhizome + root biomass removed in the grazed samples were highly significant ($P < 0.001$) (Table 1). Variation among paired samples within species was significant in some cases: *H. wrightii* short-shoot mass ($P = 0.009$), *H. wrightii* rhizome + root mass ($P = 0.004$), *S. filiforme* rhizome + root mass ($P = 0.004$). The percentage reduction in short-shoot number, short-shoot biomass, and rhizome + root biomass during winter 1988–1989 was similar to that of winter 1987–1988 for *H. wrightii* and *S. filiforme*: approximately 80 to 95% of the short-shoot biomass and 50 to 67% of the rhizome + root biomass were removed in grazed patches. Manatees tended to remove more *S. filiforme* than *H. wrightii* rhizome + root biomass in both winters.

Grazed plot recovery

Short-shoots were counted in 14 1 m² plots located at six sites in Hobe Sound and eight sites in Jupiter Sound, in February, May, and August of 1989. Short-shoot count varied significantly by season ($P = 0.005$) (Fig. 1a). Summer short-shoot counts of *H. wrightii* and *S. filiforme* were significantly greater than winter short-shoot counts ($P = 0.001$); however, spring short-shoot counts did not differ significantly from winter counts ($P = 0.064$). Species and species by season interaction were also non-significant ($P = 0.292$ and $P = 0.550$, respectively).

Relative recovery rate differed by season: the ratio of August to February short-shoot counts was significantly greater than the ratio of May to February short-shoot counts ($P = 0.042$). Despite the fact that the mean recovery rate for *H. wrightii* was twice that of *S. filiforme* (Fig. 1b), the difference between species was of only borderline significance ($P = 0.059$). Species by season interactions ($P = 0.35$) were non-significant.

Puerto Rico

Radio tracking and field observation

Both UHF and VHF radio-location information revealed a heavy reliance on the seagrass

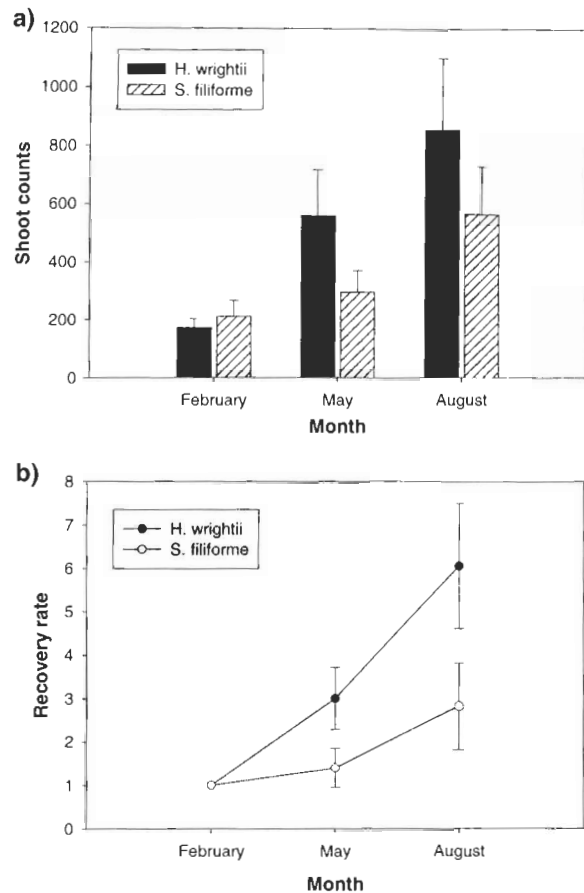


Fig. 1a. Mean number of short-shoots/m² of *Halodule wrightii* (black bar; $n = 9$ in February and 8 in May and August) and *Syringodium filiforme* (diagonal hatch; $n = 5$ in all months) in grazed plots. August shoot counts were significantly greater than February counts for both species ($P < 0.001$). Error bars = 1 S.E. Plots were located and marked within 24 h after observation of grazing by Manatees (*Trichechus manatus latirostris*) in February 1989 in Hobe Sound and Jupiter Sound, Florida, USA. Fig. 1b. Relative recovery rates of *Halodule wrightii* (open dots; $n = 8$) and *Syringodium filiforme* (black dots; $n = 5$) in grazed plots. Recovery rate was expressed as the ratio of May and August short-shoot counts to February counts. The mean ratio of May to February shoot counts was significantly less than the mean ratio of August to February shoot counts for both species ($P = 0.042$). Error bars = ± 1 S.E.

beds and near-shore waters of RRNS. Areas of high Manatee use were concentrated in the main harbour at RRNS and in shallow coves and bays protected from wave action. Four of the seven radio-tagged Manatees periodically travelled

Table 1. Mean shoot count and biomass data for Manatee grazing areas, by seagrass species, for the winter of 1988–89 in the southern Indian River Lagoon, Florida. N = the number of paired seagrass samples. Biomass means are expressed as a dry weight per m². Standard deviations of the means are given in parentheses.

Species		N	Shoot count*	Shoot biomass	Rhizome + root biomass
<i>Halodule</i>	grazed	44	189 (57.9)	2.2 (4.3)	17.8 (15.3)
<i>Halodule</i>	ungrazed	44	1 082 (280.3)	10.4 (9.8)	33.1 (30.6)
<i>Syringodium</i>	grazed	24	194 (123.0)	5.0 (9.8)	33.8 (46.3)
<i>Syringodium</i>	ungrazed	24	1 355 (111.1)	45.8 (32.1)	101.6 (76.4)

* Shoot count means were obtained by back-transformation of square-root scale means.

from eastern Puerto Rico across the channel to Vieques Island. The resulting location data showed these Manatees' preference for the seagrass beds along the north-west coast of Vieques.

Tagged Manatees were observed feeding on 126 occasions. Except for incidental consumption of macroalgae, seagrasses were the only food plants identified as forage. Of 91 feeding observations in which plant species was identified, 54 (59%) were *T. testudinum*, or mixed beds dominated by *T. testudinum*. *H. wrightii*, typically in monotypic stands, was the food plant for 35 (38%) observations. Tagged Manatees were rarely seen feeding on *S. filiforme* dominated beds.

Manatees were repeatedly observed feeding at specific locations. Although seagrass beds extend several kilometres offshore and to depths

>20 metres, most locations and all documented feeding areas were close to shore and in shallow water (Fig. 2). For 115 feeding observations in which water depth was determined, the mean depth was 2.03 m (range 1–5 m).

Indications of feeding specialization

Manatees were frequently seen feeding in Pelican Cove, a relatively small (0.6 km²) embayment at RRNS (Fig. 2). Like nearly all of the mapped subtidal areas on RRNS, the cove's dominant seagrass is *T. testudinum* except in the centre portion, where *H. wrightii* alone occurs. Manatees observed grazing in Pelican Cove fed on *H. wrightii* in 29 (67%) of 43 observations. Despite the limited occurrence of this seagrass in the region, Manatees were also observed feeding on *H. wrightii* at other locations, for example, just east of Pelican Cove (Fig. 2). Typically, these were wave-scoured areas near

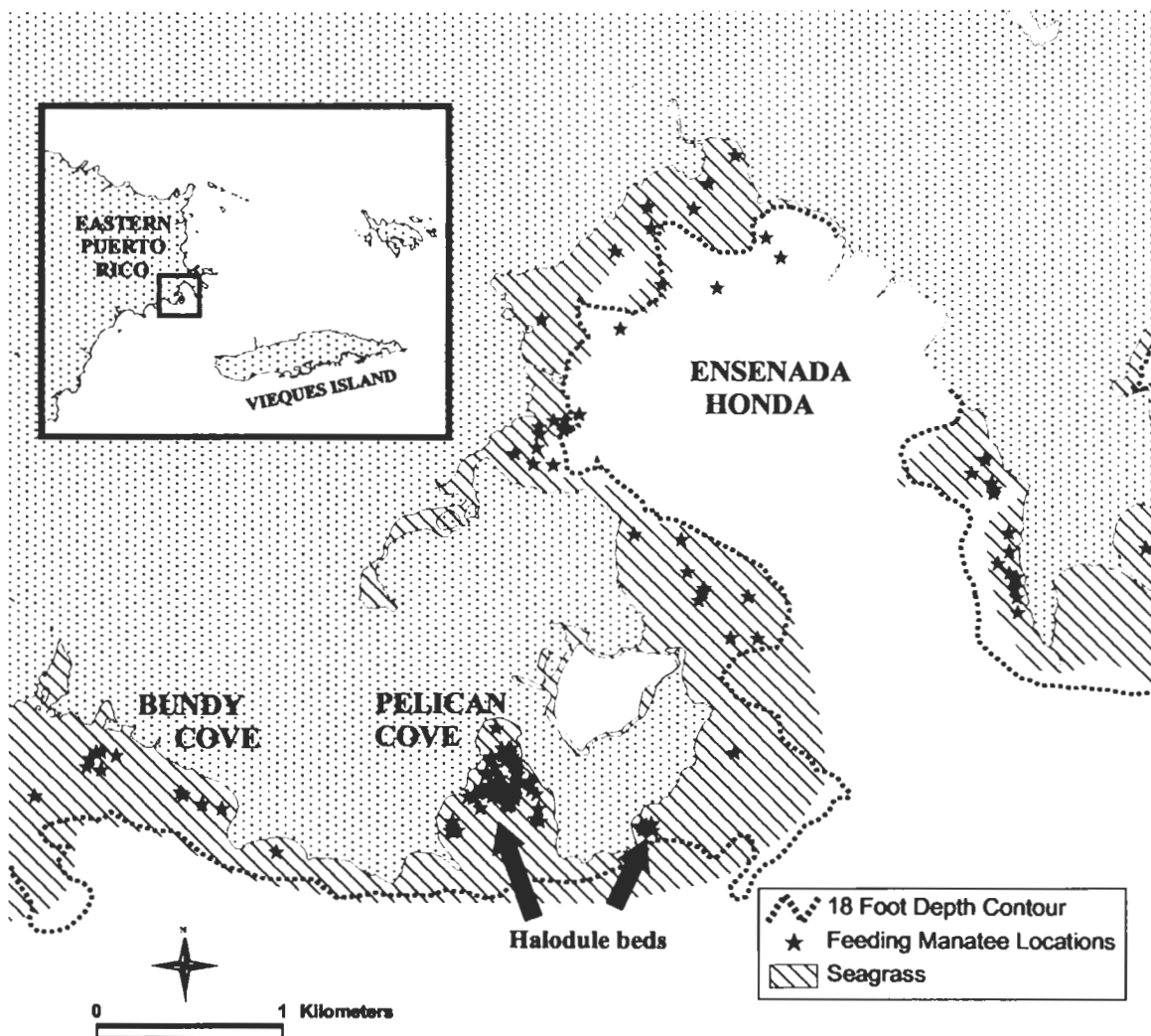


Fig. 2. Map of eastern Puerto Rico showing the Roosevelt Roads Naval station, Vieques Island, locations where Manatees (*Trichechus manatus manatus*) were seen feeding (stars), and mapped seagrass beds (diagonal hatch). Seagrass coverage was determined by photo-interpretation, and outside of Ensenada Honda, extends further offshore than is shown here. Locations are also shown for two *Halodule wrightii*-dominated grassbeds that are referred to in the text.

shore where *H. wrightii* occurred alone on sand bottom. These observations suggest that some Manatees seek out and feed in physically disturbed areas where *H. wrightii* dominates over *T. testudinum*.

Manatees were also frequently observed feeding in Bundy Cove and Bahia Algodones where *T. testudinum* dominated beds were mixed with the mound-forming calcareous algae, *Halimeda opuntia*. The genus *Halimeda* is known for its ability to form thick build-ups of sediment organized into mounds and ridges in close association with coral reefs and seagrass beds (Roberts and Macintyre 1988). Grazing Manatees overturned and pushed aside the *H. opuntia* in order to feed on *T. testudinum* shoots, ignoring adjacent *T. testudinum* beds without *H. opuntia*. A preliminary inspection revealed that *T. testudinum* leaf blades and sheaths within the clumps of *H. opuntia* were longer and wider than those from adjacent sites outside of the clumps, resulting in a 3-fold larger leaf surface area (47 v. 15 cm²; n = 10 short shoots inside and 10 outside *H. opuntia* clumps).

DISCUSSION

Indian River Lagoon

Grazing sites

Both *H. wrightii* and *S. filiforme* are restricted to depths <2.0 m in Hobe Sound and <3.0 m in Jupiter Sound (Kenworthy and Fonseca 1996). Even though seagrasses growing at these depths are readily accessible to Manatees, feeding was generally restricted to depths ≤1.6 m. The more numerous observations of Manatees feeding on *H. wrightii* than *S. filiforme* in Hobe Sound suggest that Manatees may prefer *H. wrightii*, even though short-shoot biomass of *S. filiforme* is at least twice that of *H. wrightii* in all seasons (Kenworthy 1992). The difference in per cent reduction (Table 1) of *S. filiforme* v. *H. wrightii* rhizome + root (66.7% v. 46.2% in 1989 and 58.8% v. 48.1% in 1988) suggests that Manatees are able to remove more *S. filiforme* than *H. wrightii* rhizome, either by deliberate intent, or because *S. filiforme* rhizomes are easier to excavate from the sediment. The smaller-diameter rhizomes and denser, finer roots of *H. wrightii* may be more difficult for Manatees to extract. Yet despite this disadvantage, Manatees were found more often feeding on the lower-biomass *H. wrightii*.

Alternatively, the apparent preference for *H. wrightii* may simply reflect the relative abundance of Manatee food items. An extensive benthic survey of Hobe Sound indicated that at water depths <2.0 m, *H. wrightii* was encountered 70% of the time, whereas *S. filiforme* occurred in only 29% of the samples

(Kenworthy 1992). These relative frequencies are consistent with an earlier study of Hobe Sound which reported that *H. wrightii* and *S. filiforme* comprised 66% and 28% of the seagrasses, respectively (Packard 1981). This comparison suggests the species most commonly encountered at the feeding sites remained stable for at least 10 years (Packard 1981; Kenworthy 1992). As recently as 1998, ground-truth observations supporting habitat mapping efforts in the Indian River Lagoon confirm the extent and stability of the relative species abundance in Hobe and Jupiter Sounds (Mark Finbeiner, NOAA, Coastal Services Center, Charleston, SC; unpubl. data).

Further evidence that *H. wrightii* is the most frequent component of Manatee diets in Florida was revealed by microscopic examination of the gut contents of 84 Manatees from South Florida recovered in a carcass salvage programme (Ledder 1986). *H. wrightii*, *S. filiforme*, *Ruppia maritima*, and *T. testudinum*, as well as many fresh water plants were consumed, but *H. wrightii* composed the largest portion of the Manatee's seagrass diet (24.4% v. 9.1% for *S. filiforme*). This finding is consistent with broader surveys of seagrass abundance in the Indian River Lagoon, which show that *H. wrightii* occurs more than twice as frequently as *S. filiforme* (43% v. 20%) (Virnstein *et al.* 1997).

The ungrazed reference cores (Table 1) of *H. wrightii* taken in Hobe Sound during this study had lower mean short-shoot counts (1 082 m⁻²) than the means determined for two other sites sampled in Hobe Sound in February 1989 (2 500 m⁻²) and 11 sites sampled in February 1988 (1 800 m⁻²) (Kenworthy 1992). Predictably, *H. wrightii* short-shoot biomass (10.4 gdw m⁻²) was also lower in our ungrazed samples than at the other two sites sampled in Hobe Sound in February 1989 (25 gdw m⁻²) and the 11 sites sampled in February 1988 (19 gdw m⁻²) (Kenworthy 1992). This suggests that Manatees were feeding on *H. wrightii* beds of lower density. It is possible that Manatees return to previously grazed areas which have not fully recovered in terms of numbers and biomass of shoots, but which may have other attractive attributes. Several of the aerial photographs taken during this study support our underwater observations that Manatees tended to feed on the edge of sparse *H. wrightii* beds. From the air, these light-coloured sparse patches looked like they may be old feeding scars. The observations of Manatees feeding in some of the same areas in winter 1988–1989 as in winter 1987–1988 also support the conclusion that Manatees return to formerly grazed areas to feed. Finally, although significant recovery occurred in grazed plots between February and August (Fig. 1b), the mean number of *Halodule*

shoots in August (853 m^{-2}) was similar to the mean number in ungrazed samples in February ($1\,082 \text{ m}^{-2}$), suggesting that the 1989 grazed areas would be likely to have lower than average shoot density in the subsequent winter.

Newer seagrass shoots have fewer epiphytes, less ash, and more nutritional value (Bjorndal 1980; Dawes and Lawrence 1983; Zieman *et al.* 1984). Manatees, like Green Turtles (Bjorndal 1980; Zieman *et al.* 1984), may be maintaining a source of forage of higher nutritional quality by returning to previously grazed sites with lower density, similar to what has been observed for Dugongs (Wake 1975; Anderson and Birtles 1978; Preen 1995). De Iongh *et al.* (1995) pointed out that the observed Dugong preference for sparse seagrass beds may be explained by high levels of soluble carbohydrates in the below-ground fraction of these beds. Preen (1995) noted that species composition of seagrass beds can be altered by intensive Dugong grazing, which favours rapidly growing pioneer species. He used the term "cultivation grazing" to describe the activities of large herds of Dugongs (>140 animals) feeding in the same location for weeks to months. We did not observe such intensive grazing by Manatees in Hobe or Jupiter Sound during the two winters of this study; however, previous observations suggest that this may occur in colder winters when Manatees are more abundant near warm-water refuges (Packard 1981).

Recovery from grazing

Our results indicate that Manatee grazing does not have a significant short-term negative effect on either *H. wrightii* or *S. filiforme* short-shoot regrowth in the Indian River Lagoon sites. Most of the 1 m^2 grazed plots showed significant recovery within one growing season (Fig. 1). It is certainly possible that Manatees may have a much more profound effect on grass beds in Jupiter Sound and Hobe Sound during a severe winter, when more Manatees residing in the area will result in more biomass removal over a larger area (Packard 1981, 1984). However, the similarity in seagrass bed distribution and composition reported by Packard (1981) to that found in this study indicates that seagrass beds in this region have remained stable for at least 10 years. Furthermore, Hobe Sound and Jupiter Sound are not heavily used by Manatees during the warm season, so that grazed areas probably have time to recover before being regrazed.

Comparisons of Manatee and dugong grazing activity in tropical and temperate regions

Manatees observed in both the Indian River Lagoon and eastern Puerto Rico fed more often

on the most frequently encountered seagrass: *H. wrightii* in the Indian River Lagoon and *T. testudinum* at RRNS. There were very few observations of Manatee feeding on *S. filiforme* beds in Puerto Rico, despite this species' common name of Manatee Grass. Almost all of the observations of feeding on *S. filiforme* in the Indian River Lagoon were in Jupiter Sound. Seagrasses in the Indian River Lagoon study area are restricted to depths $<3.0 \text{ m}$, and grazing occurred at depths $<1.6 \text{ m}$. Similarly, grazing of seagrasses in Puerto Rico was restricted to water depths $<5.0 \text{ m}$, although seagrasses grow to water depths $>20 \text{ m}$ throughout much of the study area. Manatees prefer sheltered waters, which is evident from the high frequency of locations in Pelican Cove (Fig. 2), and may prefer to feed in shallow depths because it is energetically more efficient. In contrast, Dugongs frequently venture much further offshore than Manatees, and utilize deeper seagrass habitat (Marsh and Saalfeld 1990; Marsh *et al.* 1994).

Several observations suggested that Manatees in Puerto Rico have developed specialized feeding behaviour. The most unique observation was Manatee removal of *H. opuntia* to feed on *T. testudinum* shoots, even though more accessible *T. testudinum* was available immediately outside of the *H. opuntia* clumps. This behaviour was described by Zieman (1982), who assumed that soft sediments associated with these sites allowed Manatees to extract more of the plants than they could at sites with consolidated sediments. However, Manatees were never observed to feed on exposed *T. testudinum* rhizomes along the edges of wave or current scoured "blowouts" in seagrass beds. We hypothesize that the larger *T. testudinum* plants growing in *H. opuntia* clumps may be more productive and of greater nutritional value to herbivores.

Manatees were also regularly observed feeding in an isolated *H. wrightii* bed in Pelican Cove. This feeding behaviour is similar to the intensive grazing in specific areas described for Dugong herds in temperate regions of Australia (Preen 1995; Anderson 1998) and smaller groups of Dugongs in a tropical ecosystem (de Iongh 1996). Manatee grazing may actually encourage the growth of smaller, faster growing species such as *H. wrightii*. However, seagrass beds in Puerto Rico also experience regular physical disturbance which could enhance the distribution and abundance of the faster growing, opportunistic species instead of *T. testudinum* (Zieman *et al.* 1989). Manatee foraging activity and wave action may alternate in the roles of primary and secondary sources of seagrass bed disturbance, reinforcing the effects on local seagrass communities. De Iongh (1996) noted

that seagrasses in tropical areas experience disturbances that may perform the same role as cultivation grazing.

We hypothesize that Manatees in Florida, which undergo seasonal migrations and utilize a much wider array of aquatic food resources, are less specialized grazers than Manatees in eastern Puerto Rico, which feed almost exclusively on seagrasses. Florida Manatees benefit the most by eating what is available in proximity to their refuges or travel routes. In contrast, Manatee distribution in eastern Puerto Rico is unrestricted by thermal regimes and the animals may have developed more specialized feeding strategies to maximize their energy intake from less diverse and less widely distributed resources. Preen (1995) hypothesized that cultivation grazing is the Dugong's response to nutritional stress resulting from seasonal declines in water temperature in subtropical and temperate regions of Australia. Unlike Manatees, Dugongs in cooler regions do not typically undergo long seasonal migrations, perhaps because of their dependence on seagrasses and reliance on localized feeding patterns. Manatees in Puerto Rico and Dugongs in Indonesia (de Iongh 1996) have also been observed returning to feed in the same *Halodule* spp. beds, suggesting that cultivation grazing by sirenians is not limited to cooler latitudes.

Integration of different approaches to study Manatee utilization of seagrass habitats

We are still in the early stages of research on Manatees as seagrass herbivores. In this paper, we have developed our understanding of Manatee-seagrass interactions by integrating results from larger-scale studies of Manatee distribution and habitat characterization with those from finer-scale research on Manatee grazing impacts. Aerial surveys are an effective tool to determine the overall distribution of Manatees in a study region, as well as to locate specific feeding sites. Satellite and conventional radio tracking techniques allow more continuous observations on the behaviour of individual Manatees. Data on bathymetry, seagrass bed distribution and composition, temperature, and salinity contribute to our understanding of Manatee habitat utilization. Use of a data-logging Global Positioning System Manatee tag is currently under development by the US Geological Survey and Lotek Marine, Inc., and will allow much more accurate determination of multiple feeding sites by radio-tagged Manatees. Valentine and Heck (1999) note in their comprehensive review of research on seagrass herbivory that there are still many unanswered questions, such as what factors control seagrass responses to grazing, and how grazing affects rates of energy flow through nearshore food

webs. More detailed field experiments are needed to determine how and why Manatees select specific feeding sites, and their role in nutrient and energy cycles.

Conservation issues

Manatees are considered endangered throughout their range (Lefebvre *et al.* 1989; Marsh and Lefebvre 1994). Without an adequate understanding of their habitat requirements and feeding behaviour it might appear that Manatees in the Indian River Lagoon and Puerto Rico have unlimited food resources. This is clearly not the case in Florida where seasonal temperature declines constrain Manatees within smaller geographic areas during periods of the winter. In Hobe and Jupiter Sounds Manatees consume the most abundant seagrasses (*H. wrightii* > *S. filiforme*), which are also relatively fast-growing species capable of recovering from grazing. But despite their rapid growth, these two seagrasses are more vulnerable than *T. testudinum* to physico-chemical disturbances (Fourqurean *et al.* 1995). They are shallow-rooted and have fewer energy reserves than *T. testudinum*, and thus are more susceptible to physical degradation and deterioration in water quality. Future efforts to protect important Manatee habitat should incorporate management issues regarding water quality and damaging physical impacts to *H. wrightii* and *S. filiforme* growing in proximity to warm water refuges and known feeding areas.

Given their association with shallow-water seagrass beds, it is not surprising that Manatees are highly vulnerable to collisions with watercraft. Watercraft collision is the largest cause of human-related Manatee mortality in Florida, and changes in watercraft design that enable boats to operate in very shallow water may increase the frequency of collisions with Manatees (Wright *et al.* 1995). Seagrass beds are also vulnerable to destruction caused by watercraft propellers and hulls (Sargent *et al.* 1995). Protection of shallow (<2 m) seagrass beds from physical damage by watercraft will benefit both seagrasses and Manatees, particularly in areas known to sustain large numbers of grazing Manatees.

In Puerto Rico, the importance of specialized feeding behaviour needs to be investigated further in order to determine if sanctuaries should be identified and managed to protect Manatees. The waters of RRNS are heavily used by Manatees and provide ample Manatee feeding and resting areas with a reliable source of freshwater. Restricted human access to the naval base provides sanctuary for Manatees in eastern Puerto Rico through security constraints on recreational boat traffic and effective Manatee protection efforts. However, frequent Manatee use of seagrass beds in Bahia Algodones, west

of Roosevelt Roads and outside the protected base waters, suggests that Manatees may be impacted by development pressures proposed for this site. The methods used in Hobe Sound to study seagrass utilization and recovery, along with mapping of seagrass species composition and the tracking of Manatee movements by telemetry, are being incorporated into a more intensive study plan designed to identify critical Manatee feeding habitats in Puerto Rico.

Sirenians and seagrasses have co-evolved over millions of years (Domning 1981), and their destinies may still be linked through the process of grazing and its ecological consequences, and through our growing recognition that to conserve either an animal or plant resource, we must conserve both. Bryden *et al.* (1998) noted, for example, that given the Dugong's highly specialized dietary requirements, only certain seagrass meadows may be suitable as Dugong habitat. Research on Manatees as grazers of seagrass communities can benefit from work in widely different environments, using both small and large-scale approaches. Seagrass mapping and Manatee habitat use studies, in conjunction with detailed field research on seagrass-herbivore ecology, will continue to help us fine-tune our recommendations for protection and management of these vital and unique marine resources.

ACKNOWLEDGEMENTS

Support for the Florida study was provided by the US Fish and Wildlife Service (USFWS), National Marine Fisheries Service, the Florida Department of Environmental Protection, the Marine Mammal Commission, Save the Manatee Club, and the Hobe Sound Nature Center. Daryl Domning, Howard University, and Tom O'Shea, US Geological Survey, contributed many helpful ideas in planning of this research. Steve and Jeannie Harris, Tequesta, Florida, generously provided free air-fills for our SCUBA tanks. Co-operators in Puerto Rico included the US Naval Station Roosevelt Roads, Puerto Rico Department of Natural Resources, the USFWS Caribbean Field Office (Boqueron, PR), the USFWS Endangered Species Office (Jacksonville, Florida), and the Caribbean Stranding Network. Curtis Kruer (Caribbean Fisheries Consultants) participated in mapping and seagrass assessments in Puerto Rico. Dean Easton (USGS) handled digitized data and prepared the Puerto Rico figure. Daryl Domning, Helene Marsh, and John Valentine provided helpful reviews of the manuscript.

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